EUNGARION MCDONALDI GEN. ET SP.NOV., A MONTANE SEMI-SLUG FROM MIDEASTERN QUEENSLAND RAINFORESTS (PULMONATA: HELICARIONIDAE)

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Eungarion mcdonaldi gen. et sp.nov. is described from the montane rainforests of mideastern Queensland. *E. mcdonaldi* has a suite of unusual features which are discussed in relation to other eastern Australian semi-slugs and eastern Australian rainforest biogeography. ☐ *Pulmonata, Helicarionidae, Eungarion mcdonaldi, semi-slug, systematics, biogeography, rainforest.*

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The rainforests between Sarina and Proserpine, mideastern Queensland (MEQ) are significant land snail habitats. Many species are endemic to the region, and some are restricted to the moist uplands. Indications are that these montane habitats were important refugia for land snails in drier times (Stanisic, 1990). Snails are particularly moisture sensitive animals and utilise their shells primarily for protection from desiccation. Semi-slugs have reduced shells which have developed in response to stable, high-moisture levels, and a comparatively low calcium environment (Solem, 1978). Eastern Australia provided favourable habitats for semi-slug evolution during the late Tertiary and Quaternary and, today, helicarionid semi-slugs are particularly diverse in this region. The species display varied degrees of shell reduction, ranging from a reduced shell which is complete and still provides shelter for the animal, e.g. *Helicarion rubicundus* of Tasmania (Dartnall & Kershaw, 1978) to a flat, plate-like, almost internalised shell (e.g. *Parmacochlea fischeri* Smith, 1884, of northeastern Queensland). Between these extremes are a number of species with highly membranous, lenticular shells in which the internal walls of the early shell whorls are incomplete. *Eungarion mcdonaldi* gen. et sp.nov. from the summit refugia of the Clarke Range, MEQ, is one of these.

This paper details the morphological features of *E. mcdonaldi* and relates them to other eastern Australian semi-slugs. It also places the species in biogeographic context. The study is based on specimens in the Queensland Museum (QM).

SYSTEMATICS

Helicarionidae

Eungarion gen. nov.

Previous Studies

The only semi-slug previously described from MEQ is *Fastosarion superba* (Cox, 1871). It was described from Mt Dryander but, according to Queensland Museum records, also occurs in the Clarke Ra. Iredale (1933) created the monotypic *Fastosarion* for this species on the basis of shell features. Smith (1992) considered that *Fastosarion* included *Vercularion* Iredale, 1933 (type species: *Helicarion bullaceus* Odhner, 1917) and also added to it several subtropical and tropical species. The extent of the *Fastosarion* radiation needs rigorous testing by revisionary studies, but unpublished work (R.C. Kershaw, pers. comm.) shows that at least *F. superba* and *F. bullaceus* may be closely related.

Diagnosis

Shell small, glossy, poorly calcified with membranous base and incomplete internal whorls. Shell sculpture obsolete. Animal with long and slender foot; caudal horn prominent. Shell lappets and mantle lobes well developed. Genitalia with epiphallic caecum and flagellum. Penis with sheath, internally pustulose and with conical verge. Spermatophore with a thin chitinous tail, otherwise without ornamentation. Radula with increased numbers of marginal teeth.

Etymology

From Eungella (the township near the type locality) and helicarion (the epithet most commonly applied to this group of semi-slugs).

TYPE SPECIES

Eungarion mcdonaldi sp.nov.

COMPARISONS

Reduced shell size, absence of shell sculpture and the degenerate nature of the shell (poor calcification, incomplete early shell whorls, membranous shell base) are features which separate *Eungarion* from *Fastosarion* Iredale, 1933. The pustulose internal penial sculpture of *Eungarion* (Fig. 4c) contrasts with the pattern of obliquely arranged, thin longitudinal pilasters seen in *Fastosarion superba* (Cox, 1871) (Kershaw, pers.comm.). *Eungarion* shows a similar level of shell reduction to that seen in the north-eastern Queensland *Thularion* Stanisic, 1993, but differs in key shell features such as sculpture, size and degree of calcification. Anatomically, the much stronger development of shell lappets and mantle lobes, lack of a prominent caudal horn and absence of a penial verge in *Thularion* are key differentiating features.

Eungarion mcdonaldi sp.nov.
(Figs 1-5)

ETYMOLOGY

Named for Keith McDonald, Conservation Strategy Branch, Queensland Department of Environment and Heritage, for his invaluable assistance in providing specimens and field data on Queensland land snails.

COMPARATIVE REMARKS

Eungarion mcdonaldi (Fig. 2) is readily distinguished from the sympatric *Fastosarion superba* (Cox, 1871) by its smaller size and degenerate shell. *F. superba* is one of the largest semi-slugs in eastern Australia (approx. animal length = 50-70mm) and has a less reduced shell with prominent spiral sculpture. In the juvenile state the shell features are also useful discriminating features.

MATERIAL EXAMINED

HOLOTYPE: QMMO43309, Dalrymple Heights, Eungella NP, MEQ. 21°02'S, 148°36'E. 1000m, notophyll vine forest. M.J. Bishop, Nov 1976. Height of shell 4.81mm, max. diameter 11.30mm, min. diameter 8.31mm, H/D ratio 0.43, whorls 2⅞-.

PARATYPES: MEQ: QMMO43310, 35 juveniles and adults, same collecting data as holotype; slopes of Mt Dalrymple, W of Mackay, 900m, on dead leaves, simple notophyll evergreen vine forest (21°04'S, 148°35'E) (5, QMMO36087, 21 May 1990, D. & N. Potter, J. Stanisic); slopes of Mt Macartney, SW Proserpine, 900m, in discarded palm fronds, notophyll vine forest/tree ferns (20°50'S, 148°33.5'E) (1, QMMO35628, J. Stanisic, D. & N. Potter, 18 May 1990); Mt Dalrymple, Eungella NP, in cave in rainforest (1, QMMO43307, V. Hansen, 19 Aug.1975).

DIAGNOSIS

Shell small, glossy, maximum diameter 9.74-11.30mm (mean 10.46mm), minimum diameter 7.14-8.31mm (mean 7.76mm), lenticular, very thin, poorly calcified. Whorls 2⅞, rapidly expanding. Body whorl expanded, not descending in front, with basal margin membranous. Spire and apex flat. Height of shell 3.25-4.81mm (mean 4.26mm), H/D ratio 0.33-0.44 (mean 0.41). Protoconch (Fig. 3a) of 1¼ whorls, smooth except for very faint growth ridges. Post-nuclear sculpture (Fig. 3b) of weak, arcuate, radial growth ridges. Sutures weakly impressed to flat. Whorls rounded above the periphery, with internal walls, membranous and incomplete. Colour yellow to golden, apex creamy-white. Based on 4 measured adults (QMMO43309, QMMO43310).

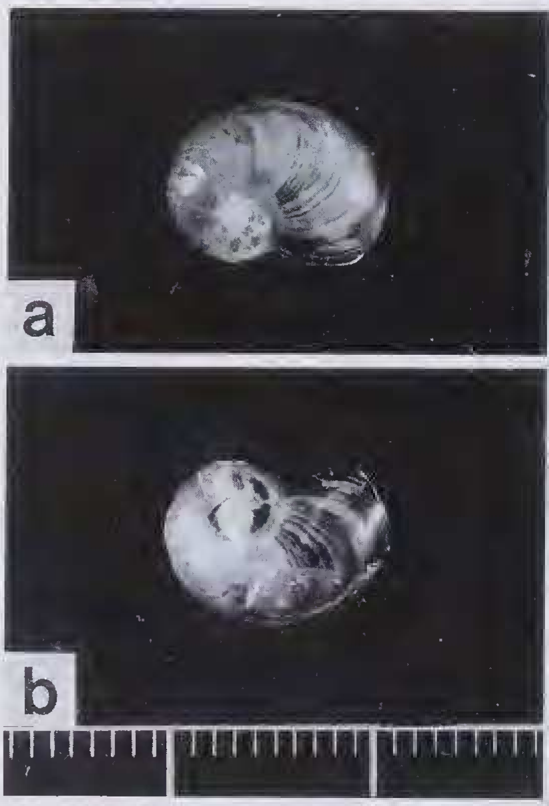

FIG. 1.Holotype of *Eungarion mcdonaldi* sp.nov., QMMO43309. a, top view; b, bottom view. Scale in mm.

Animal (Fig. 4a) small, body length (in preservative) 24.1-33.7mm (mean 29.9mm, n=5). Foot long, slender, tripartite, broadly rounded anteriorly, tapered posteriorly. Tail long, keeled mid-dorsally, with a prominent caudal horn. Caudal foss a long vertical slit in tail. Pedal grooves typically aulacopod and united above the tail. Colour (in live) reddish-brown on foot, neck, tentacles, and mantle lobes; visceral hump yellow; shell lappets pale with darker reddish-brown circular markings, also present in preserved specimens. Body ornamentation strongly developed on tail and in neck region; shell lappets with widely spaced subcircular pustulations, mantle lobes smooth. Right mantle lobe (RML) small, subtriangular, fused to right shell lappet posteriorly; left mantle lobe (LML) large, tapered posteriorly, weakly developed anteriorly and fused to left shell lappet. Right shell lappet (RL) large, subcircular, weakly fused with left shell lappet posteriorly; left shell lappet (LL) semi-circular, fused to narrow mantle collar anteriorly.

Genitalia (Fig. 4b) with multilobate, creamy-coloured ovotestis (G) embedded in the apical whorls of a dark-brown digestive gland (Z). Hermaphroditic duct (GD) swollen and convoluted. Talon (GT) with spherical head and short stalk. Carrefour (X) sub-ovoid, white. Albumen gland (GG) a multilobate mass of creamy-brown acini. Prostate (DG) a band of creamy-white alveoli appressed to the surface of a sacculate uterus (UT). Vas deferens (VD) arising from the prostate - uterus as a thin tube, descending to the peniovidual angle then ascending a short distance before entering a much thicker, muscular reflexed epiphallus (E). Epiphallus longer than penis, with a long, apical flagellum (EF) and a large epiphallic retractor caecum (ERC) arising mid-length; internally with longitudinal rib-like thickenings below level of caecum, pustulose above. Penial retractor muscle (PRM) short, attached to epiphallus adjacent to caecum. Penis (P) relatively short, cylindrical, muscular with a thick sheath (PS) surrounding the lower two-thirds; internally (Fig. 4c) with bold, nodulose pustules apically, becoming transversely elongate basally and two pustulose longitudinal pilasters (PP). Epiphallus entering penis through a smooth, conical verge (PV) that has a terminal pore (EP). Male terminal genitalia enveloped in a thin connective sheath. Vagina (V) short with sub-apical entrance of free oviduct; internally with fleshy longitudinal thickenings. Free oviduct (UV) twice as long as vagina, internally with transverse spongy folds. Spermatheca (S) with a short ex-

FIG. 2.Animal of *Eungarion mcdonaldi* sp.nov. Mt Macartney, MEQ, QMMO35628.

panded stalk (SS) inserted at the base of the free oviduct and subovate head attached about halfway along the uterus. Atrium (Y) short.

Spermatophore (Fig. 4d, SP) elongately ovoid with a long chitinous tail.

Radula with a tricuspid central tooth (Fig. 3d) that has a broadly lanceolate mesocone and two small, pointed lateral cusps; lateral teeth (Figs 3d,f) strongly bicuspid with endocone reduced to a small point high up on the edge of the mesocone, ectocone short and pointed, anterior edge irregularly grooved and ridged; marginals (Fig. 3e) bicuspid with two, equally short, pointed cusps and a long sinuate shaft. Latero-marginal transition abrupt. Basal plates of central and lateral teeth short, squarish with lateral ridges. Interrow support (Fig. 3f) provided by interlock of basal plates with anterior edge of tooth behind. Jaw (Fig. 3c) arcuate with low, concentric growth ridges. Radular formula. 140.11.1.11.140.

Based on 4 dissected specimens (QMMO-35628, QMMO43309, QMMO36087).

RANGE AND HABITAT

Known from only simple notophyll vine forests of the summits and near summits (900-1200m) of the Clarke Ra., MEQ (Fig. 5). The absence of the species from the Conway Ra. and Mt Dryander to the north, is probably real. Considerable collecting has been undertaken in these areas. *E.mcdonaldi* has been collected from inside discarded palm fronds and on leaves on the ground.

REMARKS

Relationships of *E. mcdonaldi* are not clear. A number of other semi-slugs in both northeastern and southeastern Queensland are altitudinally restricted and have degenerate shells. These will need to be dissected in order to determine whether 'very reduced-shell' forms are derivatives of local semi-slugs with more complete shells or whether they are in fact closely related species that have been separated by climatically-induced habitat fragmentation.

DISCUSSION

The eastern Australian semi-slug fauna (family Helicarionidae) is largely undescribed. Based on the collections of the Queensland Museum, it is likely that the number of species, currently 25 (Smith, 1992), will at least double. Of the named species, only a handful have been studied to a standard acceptable in modern systematics. Generally there has been undue emphasis on gross shell characters, in a group displaying a diverse range of shell reduction, to the detriment of anatomical studies. The distribution of the eastern Australian semi-slugs is mainly focussed around the archipelago of rainforest refugia occurring along the eastern edge of the continent. This is not surprising in view of their moisture sensitivity, and suggests a complex evolutionary history since their ancestors reached the continent from the Indo-Malay region in the mid-Miocene (Bishop, 1981). Sympatry involves 2, rarely 3-4 species, and there is considerable microhabitat diversification among the sympaters. Microsympatry has yet to be observed. There are no identifiable large, local radiations (Stanisic unpubl.) so that ordering of character states and identifying direction of character change probably hinges on revision of the entire semi-slug fauna. Against this background attempts to draw relationships between *E. mcdonaldi* and other described helicarionid semi-slugs need to be tempered with caution.

The use of shell characters in a group most remarkable for degrees of shell reduction requires a focus on fundamental features (Fig. 1) such as sculpture and coiling pattern rather than gross similarity. Hence, although the shell of *Thularion semoni* (Martens, 1894) from the Wet Tropics, NEQ, also has incomplete early whorls, poor calcification and membranous shell base (Stanisic, 1993) these alone are not sufficient to warrant close association with *E. mcdonaldi*. The shell of *E. mcdonaldi* is rounded, and, apart from its flattened spire and degenerate nature, more closely resembles the shell of *Helicarion* s.s. and *Fastosarion* sensu Smith (1992). Sculpture (Fig. 3a-b) is obsolete, but this should be viewed in the context of shell reduction and the concomitant loss of key features. Although reduced, the shell of *T. semoni* retains typical helicarionid spiral sculpture on both protoconch and post-nuclear whorls and has a much more expanded final whorl which gives the shell an elliptical aspect.

The animal of *E. mcdonaldi* (Figs. 2,4a) has retained the basic features (reasonably discrete shell lappets and mantle lobe, prominent caudal horn) seen in temperate species (Dartnall & Kershaw, 1978; Kershaw, 1979, 1981) and some subtropical *Fastosarion*. In contrast *T. semoni* has the lappets and lobes more fused and greatly expanded anteriorly to form a cephalic shield. Stanisic (1993) considered this exuberant development of the accessory respiratory surfaces in *T. semoni* as an evolutionary experiment intermediate between the *Helicarion* s.s. and *Parmacochlea* Smith, 1884.

E. mcdonaldi differs from southern species assigned to *Helicarion* s.s. such as *H. nigra* (Quoy and Gaimard, 1832), *H. rubicundus* (Dartnall and Kershaw, 1978) and *H. cuvieri* Ferussac, 1821, in genital anatomy (Fig. 4b-d), by possessing an epiphallic retractor caecum and lacking an epiphallic gland. The penis of *E. mcdonaldi* has a verge and simple sculpture of discrete pustules contrasting with the pattern of penial papilla and complex penial sculpture seen in the southern species (Dartnall & Kershaw 1978; Kershaw 1979, 1981). The relatively simple spermatophore of *E. mcdonaldi* is also quite distinct from the heavily ornamented (spined) spermatophores seen in *H. nigra*, *H. rubicundus* and *H. cuvieri*. I consider these to be fundamental differences above the level of changes associated with species interactions. In contrast, *E. mcdonaldi* shares some basic anatomical features with *T. semoni* (e.g. shape of spermatophore and presence of an epiphallic retractor caecum). *T. semoni* lacks a penial verge but retains pustular sculpture in the penis chamber (Stanisic, 1993). The highly modified *Parmacochlea* from far north Queensland possesses pustular penial sculpture, penial verge, epiphallic caecum and has a spermatophore not unlike that of *E. mcdonaldi* and *T. semoni* in shape. It differs only in having fine spination on the chitinous section (Simroth, 1898).

Hence there are several basic differences which separate the tropical and temperate semi-slugs. At the same time, I do not necessarily consider *E. mcdonaldi* and *T. semoni* close relatives. Whereas *T. semoni* appears to represent a distinct lineage of semi-slug development (Stanisic 1993), *E. mcdonaldi* can be readily derived from species with less reduced shells by simple but more extensive reduction in shell.

The radulae of eastern Australian semi-slugs

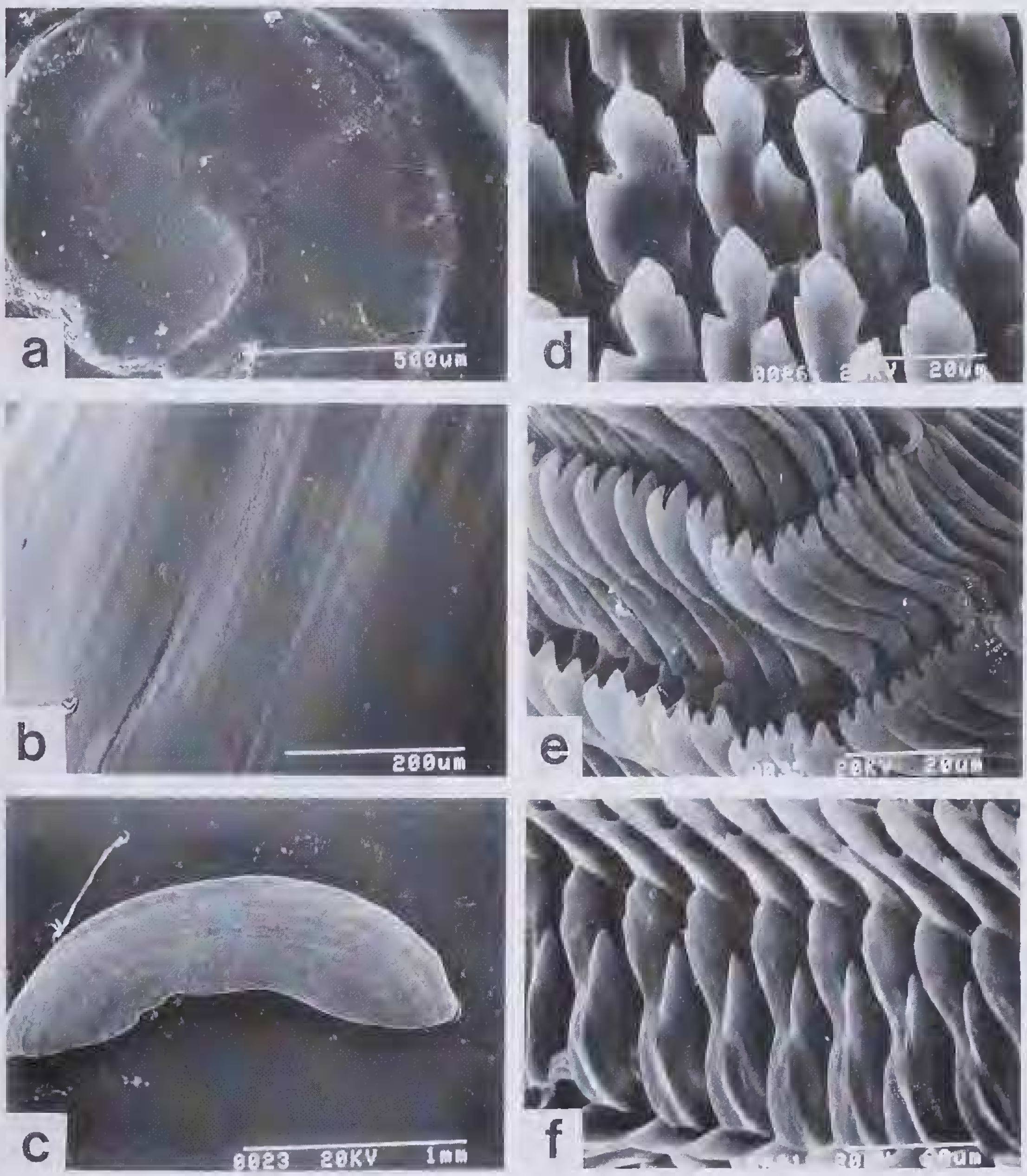

FIG. 3. *Eungarion mcdonaldi* sp.nov. Mt Dalrymple, MEQ, QMMO36087. a, protoconch; b, adult shell sculpture; c, jaw; d, central and inner lateral teeth; e, marginal teeth; f, lateral teeth showing interrow support. Scale lines as marked.

appear to be fairly generalised (Baker, 1941; Dartnall & Kershaw, 1978; Hedley 1893; Kershaw, 1979, 1981; Semper, 1885; Stanisic, 1993) in form and function (interrow support). Minor differences should probably relate to niche specialisation due to sympatry. *E. mcdonaldi* shows some radular differences from both the temperate species (*H. nigra*, *H. cuvieri*, *H. rubicundus*) and the tropical *T. semoni*. In *H. nigra*, *H. cuvieri*, *H. rubicundus* and *T. semoni* the marginal teeth have subequal, somewhat elongate cusps. In *E. mcdonaldi* the cusps (Fig. 3e) are very short and

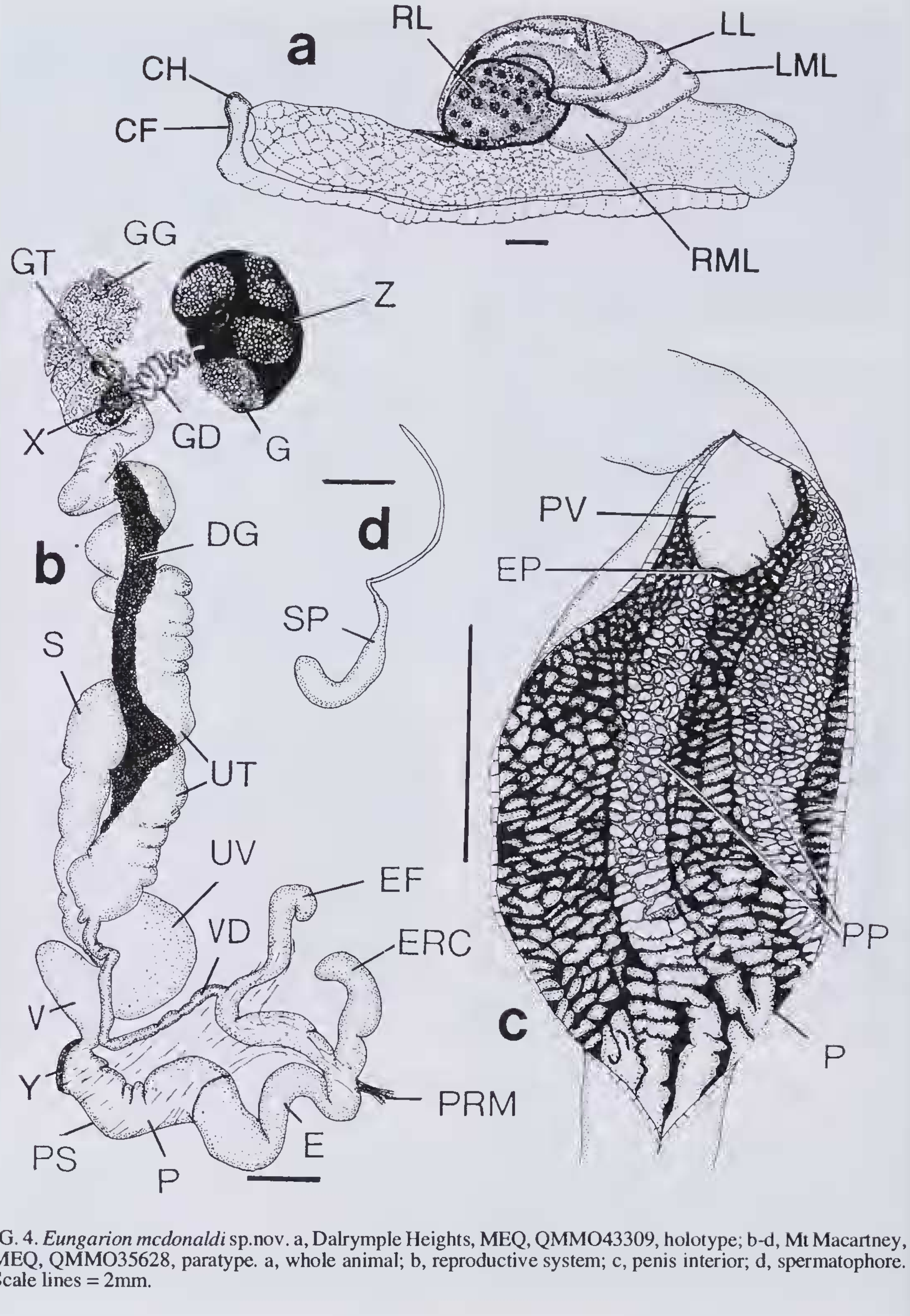

FIG. 4. *Eungarion mcdonaldi* sp.nov. a, Dalrymple Heights, MEQ, QMMO43309, holotype; b-d, Mt Macartney, MEQ, QMMO35628, paratype. a, whole animal; b, reproductive system; c, penis interior; d, spermatophore. Scale lines = 2mm.

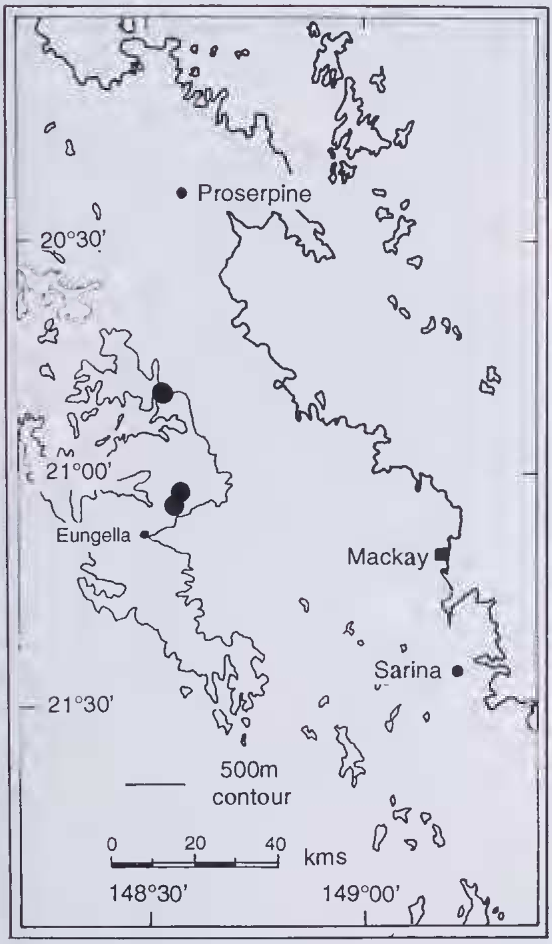

FIG. 5. Distribution of *Eungarion mcdonaldi* sp.nov. (dots).

equal. In addition, the number of marginal teeth in *E. mcdonaldi* is greatly increased (140) when compared with *H. nigra* (38), *H. cuvieri* (30), *H. rubicundus* (80) and *H. semoni* (83). While it is possible that these features may be phylogenetically significant it is also probable that they are merely related to feeding specialisation by *E. mcdonaldi* in response to its sympatry with *Fastosarion superba* (Cox, 1871).

The distribution of *E. mcdonaldi* (Fig. 5) in the summit refugia of the Clarke Ra. suggests that it has been restricted in drier times and has become environmentally-cornered. Hence, its nearest relatives may not survive in MEQ. These refugia are also home to other restricted endemic land snails, e.g. *Setomedea janae* Stanisic, 1990; *Biomphalopa recava* (Hedley, 1912) and the slug-like caryodid, *Pandofella whitei* (Hedley, 1912). With the exception of *B. recava*, which also occurs at lower altitudes at Finch Hatton Gorge, they are confined to these upland refugia. Relationships of these relict species are both with the south (*P. whitei*, *S. janae*), or north (*B. recava*, *S. janae*) and not locally, providing evidence of past connections between regions now separated by tracts of dry, snail-poor countryside. It is possible that the nearest relatives of *E. mcdonaldi* will be similarly located. At a subregional level these restricted taxa are key elements of a largely endemic MEQ snail subfauna (Stanisic, unpubl.).

The Charopidae and Caryodidae are Gondwanan groups and occurrences of family relicts in the MEQ montane communities highlight the importance of these refugia to the persistence of ancient land snail faunal elements in the region. The discovery of the restricted *E. mcdonaldi* extends their significance to modern groups.

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